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22

23 **Abstract**

24

25 Over the past decade, the abundance of sika deer has rapidly increased around Japan.
26 Previous studies have showed overabundance of deer causes drastic reduction of forest
27 understory vegetation, leading excessive soil erosion. However, no study has
28 investigated the effects of excessive deer browsing on aquatic insect assemblages via
29 sediment runoff. These effects are important to understand whether the terrestrial
30 alteration by deer influences aquatic ecosystems. In a primary deciduous forest
31 catchment in Ashiu, Kyoto, a deer exclusion fence has been in place since 2006. We
32 compared forest floor cover, overland flow, stream environment, and aquatic insect
33 assemblages in first-order streams and catchments inside and outside of the deer-
34 enclosure from May-2008 to April-2009. The floor inside the deer-enclosure catchment
35 was covered by lush understory vegetation, whereas outside was almost bare. The
36 overland flow runoff rate at midslope and the dominance of fine sediment deposition in
37 the streambed were higher outside than inside. Among aquatic insects, burrowers,
38 which are tolerant against fine sediment deposition, were significantly more abundant
39 outside than inside, whereas clingers exhibited the opposite patterns. Collector-
40 gatherers, which feed on fine detritus, were significantly more abundant outside than
41 inside. Meanwhile, filterers were more abundant inside. The Simpson's diversity index
42 of the aquatic insect assemblages was higher inside than outside. These results suggest
43 that the demise of understory vegetation due to excessive deer browsing has indirectly
44 caused changes in the aquatic insect assemblages of this catchment via increased
45 sediment runoff and subsequent sandy sedimentation of the streambed.

46

47 **Key words**

48

49 Burrowers • Clingers • Diversity • Sedimentation • Soil erosion

50

51 **Introduction**

52

53 Deer populations are increasing in many countries due to various factors such as the
54 extinction of predators, moderation of the winter climate, decreased hunter populations,
55 and strengthening of game laws (Côté et al. 2004). Increased deer populations can cause
56 reductions in preferred plants, increases in deer-resistant plants, and declines in plant
57 diversity (e.g., Fuller and Gill 2001; Gill and Beardall 2001; Rooney 2001; Horsley et
58 al. 2003; Casabon and Pothier 2008). Population of sika deer (*Cervus nippon*
59 Temminck) has increased in many places of Japan since 1980s (Miura and Tokida
60 2008). Excessive sika deer browsing directly affects plant communities by denuding
61 forest floor vegetation (Takatsuki and Gorai 1994), stripping tree bark and causing tree
62 death (Akashi and Nakashizuka 1999), damaging shrubby bamboo stands (Yokoyama
63 and Shibata 1998), seed predation (Asada and Ochiai 1996), and inhibiting tree
64 regeneration (Nomiya et al. 2003).

65 Excessive deer browsing can also lead to the devastation of natural vegetation and
66 the alteration of soils. For example, denuded understory vegetation causes runoff of soil
67 and litter (Furusawa et al. 2003) as well as changes in the physical properties of forest
68 soil (Miyashita et al. 2008; Yanagi et al. 2008). Understory vegetation protects soil from
69 becoming encrusted by the impact of raindrops; thus, understory vegetation sustains the

high infiltration capacity of forest soil (Onda and Yukawa 1994; Gomi et al. 2008). Consequently, the denudation of the understory accelerates the discharge of infiltration excess (Hortonian) overland flow, in turn causing soil erosion (Horton 1945; Sidle et al. 2007; Gomi et al. 2008). Several previous studies have demonstrated that such soil erosion occurs in areas where understory vegetation has been denuded by excessive deer browsing (Miyashita et al. 2008; Wakahara et al. 2008).

Small catchments, which contain first-order streams, are located at the top, precipitous edges of rivers, and are the most active geomorphic development areas in river basins because of erosion and landslides. Therefore, active sediment supply originating from terrestrial slopes in these catchments greatly influences the environmental and ecological systems of first-order streams. Sediment runoff alters not only turbidity but also stream substrates, both of which may affect stream communities (e.g., Rabení and Minshall 1977; Minshall 1988). In headwater systems, riparian forests also influence aquatic insect communities in streams by controlling solar radiation and temperature (Richardson and Danehy 2007); providing litter and cladoptosis, which are sources of food and case materials; and creating multiple habitats through the production of woody debris (Richardson and Danehy 2007). Aquatic insects represent various life form types and functional feeding groups, as they have adapted to diverse stream microhabitats and food resources (Takemon 2005; Merritt et al. 2008). These insects play important roles in sustaining river ecosystems, functioning as decomposers, primary consumers, prey for fish and other predators, and agents transporting organic matter from stream to terrestrial ecosystems (Covich et al. 1999). Because aquatic insect communities are vulnerable to various environmental changes, the status of these organisms is often used as an index of river health (e.g., Robinson and Minshall 1986;

94 Zweig and Rabeni 2001; Rainbow 2002; Heino et al. 2003; Matthaei et al. 2006;
95 Yoshimura 2007).

96 As noted above, excessive deer browsing accelerates soil erosion in small forested
97 catchments. In this study, we examined whether such consequences of deer browsing
98 affect aquatic insect communities. To test this question, we compared forest floor cover,
99 overland flow, stream environment, and aquatic insect assemblages inside and outside
100 of a deer enclosure in a cool-temperate primary forest in Japan. We then discuss the
101 effects of excessive deer browsing on aquatic insect assemblages in first-order streams.

102

103 **Materials and methods**

104

105 **Study site**

106

107 This study was conducted in the first-order streams of the Yura River at the Ashiu
108 Forest Research Station, Field Science Education and Research Center, Kyoto
109 University (35°20'N, 135°45'E; Fig. 1). Average annual precipitation and temperature
110 were 2,298 mm and 11.9°C, respectively, from 1976 to 2005 at the Ashiu Research
111 Station. Maximum snow depth in winter exceeds over 2 m around the study site, and the
112 ground is covered with snow from mid-December to early April. The geological
113 components of the area are sandstone, mudstone, and shale of the Tanba Belt of the
114 Mesozoic. Most of the soil is brown forest soil.

115 Excessive deer browsing has become a serious problem at the study site since the late
116 1990s (Tanaka et al. 2008) and has caused drastic decreases in the abundance and
117 diversity of understory plants (Kato and Okuyama 2004). Recent minimum-maximum

population density of deer in the study site, estimated by block count during two days in December, were; 2.30-4.21 (2006), 0.00-5.30 (2007), 1.15-5.75 (2008), 0.00-5.75 (2009), 4.60-13.80 indiv. / km² (2010) (A. Takayanagi, unpublished data). A catchment in the natural deciduous forest (area: 1.15 ha) has been fenced to exclude deer since 2006 (Fig. 1). The 2.5-m-high fence is constructed of poles and nets. No deer had invaded inside the fence during the study period according to monthly fence maintenance and visual survey of deer browsing scar along the fence (A. Takayanagi, unpublished data). Understory vegetation in the exclosure catchment had recovered well by 2008, whereas vegetation outside the exclosure has remained almost denuded.

Outside the deer exclosure in a neighboring valley, we selected a control catchment (area: 1.66 ha) (Fig. 1). The plant community structures at the exclosure and control catchments had been very similar at the start of deer exclusion (Sakaguchi et al. 2008), and water temperature and quality in the streams at each catchment were almost same (Table 1 and Fukushima and Tokuchi 2008). To clarify the indirect effects of excessive deer browsing on aquatic insect assemblages as much as possible, the selected two catchments were adjoining and have topographically similar streams in the same way of the antecedent control experiments (e.g., Allan 1982; Christopher and Minshall 1986; Matthaei et al. 2006). We compared forest floor cover, overland flow, environmental stream characteristics, light conditions, periphyton abundance, and aquatic insect assemblages between the exclosure and control catchments (EC and CC, respectively). The first-order streams in each catchment contain permanent water. Both catchments are covered by primary cool-temperate deciduous forests dominated by *Aesculus turbinata* Blume, *Quercus crispula* Blume, *Fagus crenata* Blume, *Clethra barbinervis*

141 Sieb. et Zucc., *Acer palmatum* subsp. *matsumurae* (Koidz) Ogata, *Pterocarya rhoifolia*
142 Sieb. et Zucc., and *Cryptomeria japonica* var. *radicans* Nakai.

143

144 Forest floor cover and overland flow

145

146 One belt transect (1 m wide) from the valley floor to 30 m up the upper slope was
147 established on the left bank of each catchment. The belt transect, which was oriented to
148 include representative vegetation of each catchment, was divided into fifteen 1×2 m
149 plots, and coverage of understory vegetation in every plot was recorded by visual
150 observation. Then, abundance and number of understory plant species in the belt
151 transect was also recorded. The survey was conducted in June and August 2008.

152 To evaluate the quantity of litter in each catchment, we collected litter in four
153 randomly selected quadrats along the downhill slopes of each catchment in August and
154 November 2009. Collected litter was dried at 60°C for 24 h and then weighed.

155 Runoff plots (0.5×2.0 m) were established at the midslopes of each catchment.
156 Plastic borders were inserted about 5 cm into the soil along all sides of the plots, and a
157 trough was inserted several centimeters into the soil (parallel to the slope direction) to
158 collect storm runoff. Runoff from these plots was routed to a rain gauge (Davis
159 Instruments, Rain Collector II) to estimate discharge per 5 min (Fig. 1). Precipitation
160 was measured by a rain gauge (Davis Instruments, Rain Collector II) situated in an open
161 area (Fig. 1). Overland flow and precipitation were monitored from June to November
162 2009. We defined rainfall event as rainfalls whose total precipitations were more than
163 10 mm and there is no rain during at least 3 h before and after the rainfall. In addition,
164 we classified rainfall event into three types (1) intermissive, (2) continual and (3) one-

peak rainfall events. If a rainfall event has over 15-min-intermission of rainfall more than four times, we regard the rainfall event as intermissive rainfall event. If a rainfall event continues with no intermission above noted, and has more than one peak, the rainfall event is regarded as continual rainfall event. If the rainfall has only one peak, the rainfall is regarded as one-peak rainfall event.

Aquatic insects

Four quadrats were set with a surber net (25 × 25 cm, 0.5-mm-mesh sieve) in the streams in each catchment. Each sampling point was located over at least a 50-cm-wide stretch of the streams, at locations where some very coarse gravel was distributed. Sediments with benthic animals in each quadrat were collected into the surber net, and as many animals as possible were collected after being placed into white vats. Collections were conducted every month from May to November 2008 and in April 2009. Collected animals were preserved immediately in 70% ethanol. Aquatic insects were separated out and classified using a stereomicroscope (Nikon SMZ800) following Kawai and Tanida (2005) and Merritt et al. (2008). Because all identified taxa were not classified to species, the number of species was underestimated. Identified aquatic insects were sorted by life form type (swimmers, crawlers, clingers, or burrowers) and functional feeding group (shredders, filterers, collector–gatherers, predators, or grazers) based on Takemon (2005) and Merritt et al. (2008).

In general, aquatic insect distribution is ultimately structured by physical-chemical tolerance of individuals in the population (Cummins et al. 2008), and fecundity of aquatic insects is precisely determined by temperature (Vannote and Sweeny 1980;

Rader and Ward 1990). Individuals of aquatic insects are distributed following their optimal temperature regime along a thermal gradient related to altitude. Therefore, we regarded aquatic insect assemblages in the EC and CC before the start of deer exclusion in 2006 as very similar structures because of their physical (Table 1 and Fig. 1), chemical (Fukushima and Tokuchi 2008) and thermal similarities (Table 1).

Environmental characteristics of the streams

The water depth in each quadrat was calculated by averaging the depths at six points in each quadrat. Current velocity at the center of each quadrat was calculated by averaging three averages of repeated 5-s measurements using a current meter (KeneK, VE10).

We used visual estimation and grain size test to evaluate streambed characteristics.

To evaluate the stream substrate, photographs were taken from 50 cm above the streambed in each quadrat. The proportion of fine sediment in each quadrat was calculated using Adobe Photoshop Elements, version 5.0. Randomly shoveled three 1000 ml stream substrates were sieved into eleven grain sizes: 63, 31.5, 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm, and dried at 105°C for 24 h and weighed. These surveys were conducted in August, September, and October 2008 except grain size test, which was conducted in December 2010. We monitored the water temperature in the terminal point of each catchment from April 2010 to November 2010 per 5 min using thermometer (Trutrack, SE-TR/WT500).

Light conditions

Hemispherical photographs were taken around the quadrats in each catchment in August 2008 and April 2009 to determine the light conditions above each streambed. The first photographs were taken in the terminal area of each catchment, and the last five were taken about 6 m from the previous point. Photographs were taken with a digital camera (Nikon E995) equipped with a fish-eye lens (Nikon FC-E8) that was fixed horizontally at 1 m above the streambed. Relative solar radiation from May to October 2008 was calculated as a measure of light conditions in the growing season using photographs taken in August. Values from November 2008 to April 2009 were calculated as light conditions in the fall using photographs taken in April. Solar radiation was estimated from photographs using Gap Light Analyzer version 2.0. Magnetic north was set at a declination of 7.20° west. The radiation component was set as the default value.

Periphyton

Four submerged rocks were randomly collected from around the quadrats in each catchment in August, September, and October 2008. Periphyton was collected by brushing 4 cm² of the upper surface of each rock and filtering the water through glass microfiber filters (Whatman GF/F). These samples were ground in 90% acetone and then centrifugally separated (Hitachi CF16RXII) after being dried and frozen. The absorbance of the periphyton samples was measured at 750, 664, 647, and 630 nm (Hitachi U-1800). The amount of chlorophyll *a* was calculated by substituting the measured values into the formula of Jeffrey and Humphrey (1975).

Statistical analyses

T tests were used to determine the differences between the EC and CC in the coverage of understory vegetation, amount of litter, water temperature, water depth, current velocity, proportion of fine sediment, relative solar radiation, and periphyton abundance. The values of coverage of understory vegetation and proportion of fine sediment were arcsine-transformed to normalize distributions and standardize variance structures.

To test for differences in aquatic insect variables between the EC and CC, a two-way analysis of variance (ANOVA) was performed using streams ($n = 2$) and sampling month ($n = 8$) as factors. For ANOVAs with significant effects, multiple mean comparisons were made using Tukey's test. Abundance data were log-transformed to normalize distributions and standardize variance structures following Yamamura (1999) prior to statistical analyses.

Results

Forest floor cover and overland flow

Vegetation cover on the hillslope was higher in the exclosure catchment (EC) than in the control catchment (CC) (Table 1 and Fig. 2), where understory vegetation was almost denuded and the soil was exposed in a large area (Fig. 2). The number of understory plant species was higher in the EC (82 species) than in the CC (31 species). Preferred plant species for deer were more abundant in the EC than in the CC whereas unpreferred species were commonly distributed both in the catchments (S1 in the

Electronic Supplementary Material, ESM). The abundances of some unpreferred plant species such as *Dennstaedtia scabra* (Wall. ex. Hook.) Moore and *Shortia uniflora* var. *kantoensis* Yamazaki were higher in the CC than in the EC (S1 in the ESM). There were 16 intermissive, 12 continual and 8 one-peak rainfall events during the monitoring period. Total runoff of overland flow during the representative rainfall event was lower in the EC compared to the CC for all three types of rainfall events (Fig. 3). In particular, the overland flow hydrographs at the CC were sharply peaked during intermissive and one-peak rainfall events. Runoff rate of overland flow during entire of the motoring period (i.e., runoff / precipitation) was 4.10% and 1.55% in the CC and EC respectively. Thus, overland flow discharge was about 2.65 times greater in the CC than in the EC.

Environmental characteristics of the streams

Water depth, current velocity, and relative solar radiation were relatively similar between the EC and CC (Table 1). However, the proportion of fine sediment in the streambed was significantly higher in the CC than in the EC (Table 1), and the grain size of particles was biased to small in the CC in comparison with that the EC (Fig. 4). The effective grain size (D_{50}) was larger in the EC than in the CC (10.3 mm vs. 6.0 mm, respectively).

Although we did not detect a significant difference in periphyton abundance between the two catchments, the average quantity of periphyton was higher in the EC than in the CC (Table 1).

Aquatic insects

285

286 A total of nine orders, 52 families, 75 genera, 111 species, and 3,311 individuals of
287 aquatic insects were collected during our surber-net samplings.

288 The number of species was higher in the EC than in the CC in May, June, November
289 and April (Fig. 5). The Simpson's diversity index was relatively higher in the EC than
290 in the CC in all sampling months (Fig. 5). In terms of aquatic insects classified by life
291 form type, the abundance of burrowers was significantly lower in the EC than in the
292 CC, whereas the abundance of clingers was significantly higher in the EC (Table 2 and
293 Fig. 6). In terms of insects classified by functional feeding group, the abundance of
294 collector-gatherers was significantly lower in the EC than in the CC, whereas the
295 abundance of filterers was significantly higher in the EC (Table 2 and Fig. 6). The
296 abundance of shredders was significantly different among sampling months in the EC
297 and CC (Table 2 and Fig. 6). Overall samples of all months in the EC contained more
298 species of Ephemeroptera and Trichoptera than those in the CC (Table 3). The
299 proportion of the five most dominant species was lower in the EC (38.7%) than in the
300 CC (43.9%) (Table 4).

301

302 Discussion

303

304 Although the plant community structure at the EC and CC was very similar at the start
305 of deer exclusion in the EC (Sakaguchi et al. 2008), diverse and abundant understory
306 vegetation has recovered in the EC, whereas the forest floor has remained nearly bare
307 outside the exclosure, including the CC (Table 1, Fig. 2). The unpreferred plant species
308 for deer were commonly distributed both in the EC and CC, and the abundances of such

plant species were relatively higher in the CC than in the EC (S1 in the ESM). These results suggest that the great differences in coverage and species richness of understory vegetation between the EC and CC were caused by excessive deer browsing.

Forest floor cover, such as understory vegetation and litter, protects the soil infiltration capacity against raindrop impact (Onda and Yukawa 1994; Gomi et al. 2008) and prevents overland flow from discharging (Sidle et al. 2007; Gomi et al. 2008). In this study, lush understory vegetation in the EC buffered the runoff of overland flow, whereas overland flow hydrographs in the CC exhibited large peaks after intermissive or one-peak rainfall events (Fig. 3). The total runoff of overland flow during all three types of rainfall events was lower in the EC than in the CC (Fig. 3). Because understory vegetation is a good predictor of soil erosion potential (e.g., Lyon and Sagers 1998; Wear et al. 1998; Heartsill-Scalley and Aide 2003), these results suggest that lush understory vegetation prevents sediment runoff and soil erosion by recharging soil infiltration capacity and consequently reducing overland flow. Although current velocity did not differ significantly between the EC and CC, the proportion of fine sediment was significantly lower in the EC (Table 1), and the grain size of particles was biased to small in the CC in comparison with that the EC (Fig. 4). These findings suggest that soil erosion on the denuded slope caused increased sedimentation of fine particles such as sand. In terms of the turbidity index, the abundance of periphyton was higher in the EC than in the CC (Table 1). Increases in light intensity are well known to cause increases in the quantity of periphyton (e.g., Hill and Harvey 1990; Wootton and Power 1993). The higher growth rate of periphyton in the EC can be attributed to less inflow of turbid water containing suspended sediment and to increases in light intensity in the stream water (Yamada and Nakamura 2002), because of no difference in light

condition (Table 1). These results suggest that the diffused fine sediment and lower abundance of periphyton in the CC resulted from active sediment runoff via soil erosion caused by excessive deer browsing of understory vegetation.

Differences in fluvial environments caused by presence or absence of deer browsing are expected to alter aquatic insect assemblages. Deposited sediment is considered a good quantifiable stressor for examining the functional responses of aquatic insects (Waters 1995). Several studies have demonstrated the effects of fine particles that fill the interstices of substrates or cover surfaces of aquatic insect habitats (e.g., Chutter 1969; Rabení and Minshall 1977; Minshall 1988; Wood and Armitage 1997; Zweig and Rabení 2001; Rabení et al. 2005).

In this study, the Simpson's diversity index was greater in the EC than in the CC among all sampling months (Fig. 5). Overall samplings contained more species in the EC than in the CC (Table 3). The insect assemblage in the CC was characterized by the dominance of sediment-burrowing ephemeropterans (e.g., *Ephemera japonica* McLachlan and *Paraleptophlebia japonica* Matsumura) and dipterans (chironomid midges of Orthoclaadiinae) (Table 4). In contrast, the assemblage in the EC was dominated by crawling plecopterans (e.g., *Nemoura* spp. and *Togoperla* sp.). All of the dominant sediment-burrowing taxa in the CC were collector–gatherers. Several studies have reported decreases in species richness caused by increases in fine sediment deposition (Zweig and Rabení 2001; Rabení et al. 2005). Our results also suggest that fine sediment deposition of the streambed causes reductions in the diversity of aquatic insect assemblages.

In terms of the life form types of aquatic insects, the abundance of burrowers was significantly higher in the CC than in the EC (Table 2 and Fig. 6). In contrast, the

abundance of clingers was significantly lower in the CC than in the EC, suggesting that gravelly substrates were less common in the CC due to sedimentation. In general, a relative tolerance to the deposition of fine sediment (< 2 mm in diameter) is strongest in burrowers, followed by climbers, sprawlers (crawlers), swimmers, and clingers (Rabeni et al. 2005). The high abundance of burrowers and the low abundance of clingers in the CC corresponded to the dominance of sandy sedimental environments (Table 1 and Fig. 4). In contrast, the high abundances of clingers and the low abundance of burrowers in the EC corresponded to the presence of gravelly sedimental environments (Table 1 and Fig. 4).

In terms of the functional feeding groups of aquatic insects, the abundance of collector–gatherers was significantly higher in the CC than in the EC, whereas that of filterers was significantly smaller in the CC (Table 2 and Fig. 6). In general, a relative tolerance to the deposition of fine sediment is strongest in shredders, followed by collector–gatherers, predators, grazers, and filterers (Rabeni et al. 2005). Our results suggest that the high abundance of collector–gatherers and the low abundance of filterers in the CC corresponded to increased fine particles deposition supplied from terrestrial slopes and increased overland flow.

In conclusion, our comparisons of aquatic insect assemblages and stream environments at sites inside and outside of a deer enclosure indicate that excessive deer browsing of understory vegetation causes increased overland flow and sandy sedimentation of the streambed, consequently altering aquatic insect assemblages. This indirect effect of deer on aquatic insects shows unexpectedly extensive effects of deer as an ecosystem engineer. Deer can alter not only a terrestrial ecosystem which they belong to, but also stream assemblages outside their original ecosystem.

381

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383

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393

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Table 1 Comparisons of average values of eleven environmental characteristics between the enclosure and control catchments. Differences between the catchments in coverage of understory vegetation, quantity of litter, water temperature, water depth, current velocity, proportion of fine sediment, relative solar radiation and periphyton abundance were tested using *t* test. Values are means \pm standard deviation.

	Exclosure catchment	Control catchment
Catchment area (ha)	1.15	1.66
Deer invasion	Deer excluded	Invasion frequent
Forest type	Deciduous forest	Deciduous forest
Coverage of understory vegetation (%)	45.40 \pm 29.36**	18.20 \pm 12.60**
Quantity of litter (g): August	79.75 \pm 24.55	47.54 \pm 23.51
: November	74.25 \pm 35.28	124.25 \pm 25.90
Water temperature (°C)	14.70 \pm 4.04	14.66 \pm 4.05
Water depth (cm)	2.35 \pm 1.76**	3.25 \pm 1.65**
Current velocity (cm s ⁻¹)	4.34 \pm 2.72	4.82 \pm 2.75
Proportion of fine sediment (%)	18.10 \pm 7.86**	36.99 \pm 9.37**
Relative solar radiation (%): August	19.31 \pm 6.88*	12.58 \pm 2.2*
: November	38.01 \pm 6.82	40.70 \pm 7.67
Periphyton abundance (mg chl. <i>a</i> 4cm ⁻²)	32.09 \pm 19.76	7.45 \pm 2.52

The same letters indicate significant differences (**P* < 0.05, ***P* < 0.01).

Table 2 Results of ANOVAs testing for effects of site and month on abundances of each aquatic insect group.

	Site		Month		Site × month	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Burrowers	14.481	<0.001	1.864	0.097	1.456	0.206
Clingers	8.869	0.005	0.585	0.765	0.843	0.558
Crawlers	3.522	0.068	1.413	0.222	2.128	0.058
Swimmers	0.015	0.902	1.779	0.113	1.264	0.288
Collector-gatherers	12.033	0.001	2.026	0.071	1.615	0.154
Filterers	6.288	0.016	0.668	0.698	0.809	0.584
Grazers	0.014	0.906	0.841	0.559	1.849	0.099
Predators	2.494	0.121	1.603	0.157	1.192	0.325
Shredders	3.265	0.077	3.535	0.004	1.556	0.172

Bold characters indicate significant differences ($P < 0.05$)

Table 3 Richness and abundance of aquatic insect of overall samples in all months in each order in each catchment.

Order	Exclosure catchment		Control catchment	
	Taxa	Indv.	Taxa	Indv.
Ephemeroptera	17	339	12	610
Odonata	7	13	8	39
Plecoptera	14	462	11	464
Coleoptera	5	77	6	49
Diptera	25	239	25	549
Trichoptera	19	206	14	231
Others	5	16	2	17
Total	92	1,352	75	1,959

Table 4 Dominant species of aquatic insect assemblages of overall samples in all months in each catchment. E, P and D in order row correspond to Ephemeroptera, Plecoptera and Diptera respectively.

Rank	Site	Order	Life form type	Feeding group	Indv.	Proportion
Exclosure catchment						
1	<i>Ephemera japonica</i>	E	Burrower	Collector-gatherer	129	9.5%
2	<i>Nemoura</i> spp.	P	Crawler	Shredder	123	9.1%
3	<i>Togoperla</i> sp.	P	Crawler	Predator	110	8.1%
4	<i>Caroperla</i> sp.	P	Crawler	Predator	82	6.0%
5	<i>Paraleptophlebia japonica</i>	E	Burrower	Collector-gatherer	81	6.0%
					Total	38.7%
Control catchment						
1	<i>Ephemera japonica</i>	E	Burrower	Collector-gatherer	298	15.2%
2	<i>Caroperla</i> sp.	P	Crawler	Predator	156	8.0%
3	<i>Paraleptophlebia japonica</i>	E	Burrower	Collector-gatherer	149	7.6%
4	<i>Nemoura</i> spp.	P	Crawler	Shredder	138	7.0%
5	<i>Orthocladiinae</i> spp.	D	Burrower	Collector-gatherer	120	6.1%
					Total	43.9%

530 **Figure Legends**

531 **Fig. 1** The study site in the Ashiu Forest, Kyoto Prefecture, Japan.

532 **Fig. 2** Landscapes at (a) the exclosure catchment (EC) and (b) the control catchment
533 (CC) on 28 June 2008.

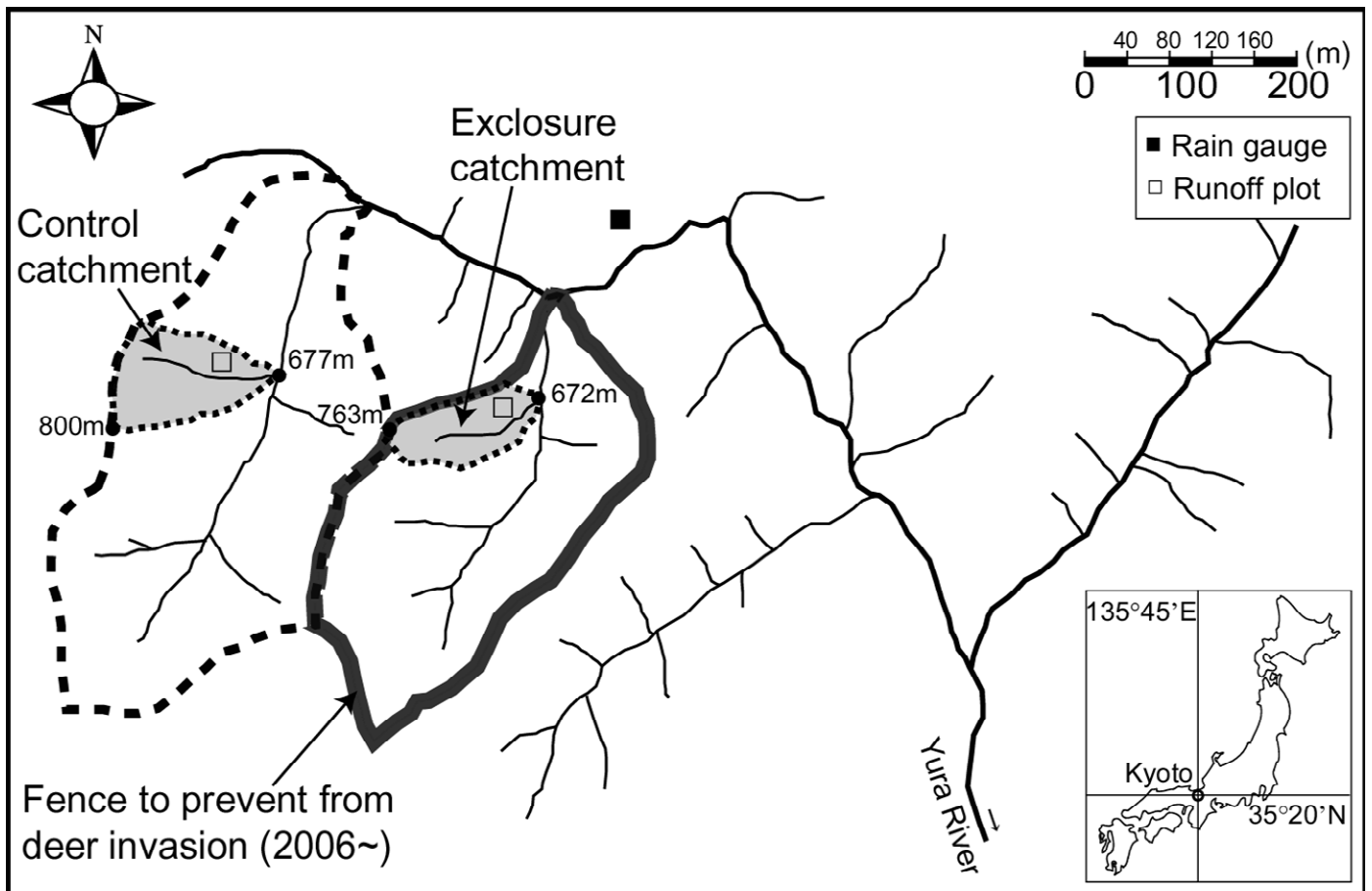
534 **Fig. 3** Representative overland flow hydrographs (mm / 5 min) at the exclosure and
535 control catchments.

536 **Fig. 4** Grain size distribution of stream substrate at the exclosure and control
537 catchments. Error bars indicate \pm standard deviation.

538 **Fig. 5** Number of species and Simpson's diversity index in each sampling month at the
539 exclosure and control catchments. Error bars indicate \pm standard deviation.

540 **Fig. 6** Abundances of four life form types and five functional feeding groups of aquatic
541 insects in each sampling month at the exclosure and control catchments. Error bars
542 indicate \pm standard deviation.

Fig. 1



(a) Exclosure catchment (EC)



(b) Control catchment (CC)



Fig. 3

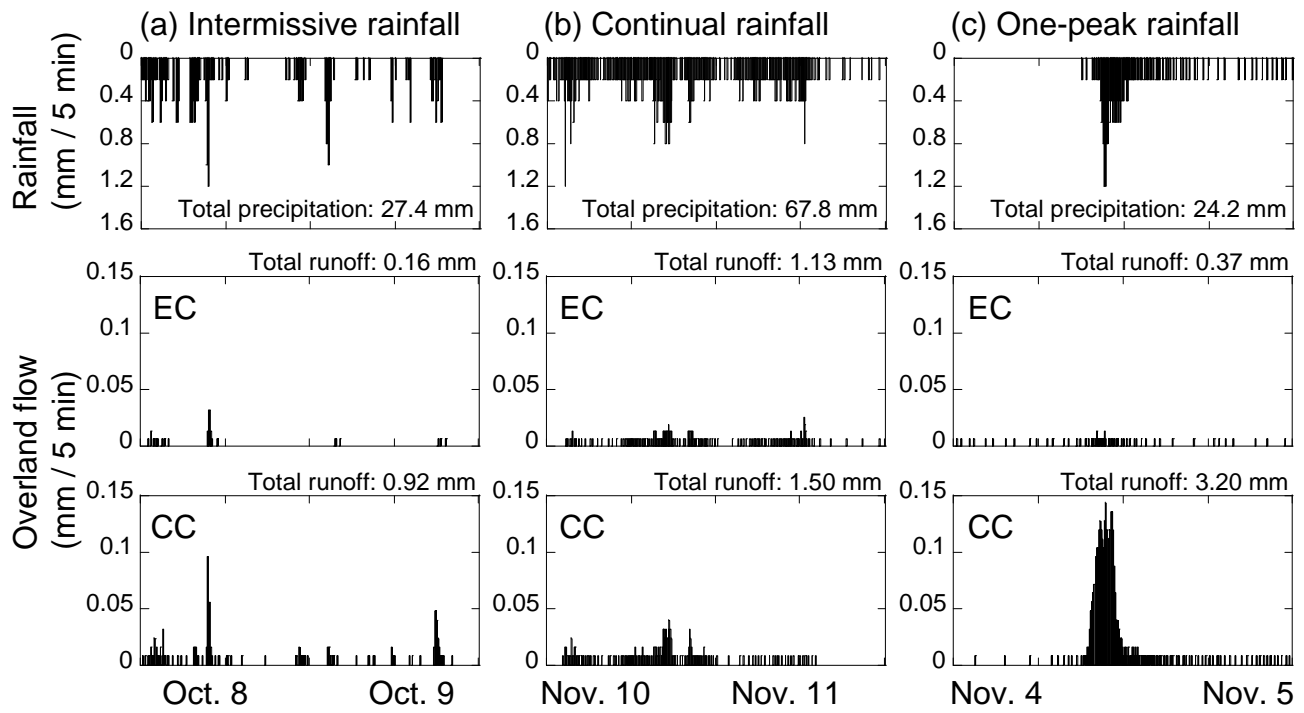


Fig. 4

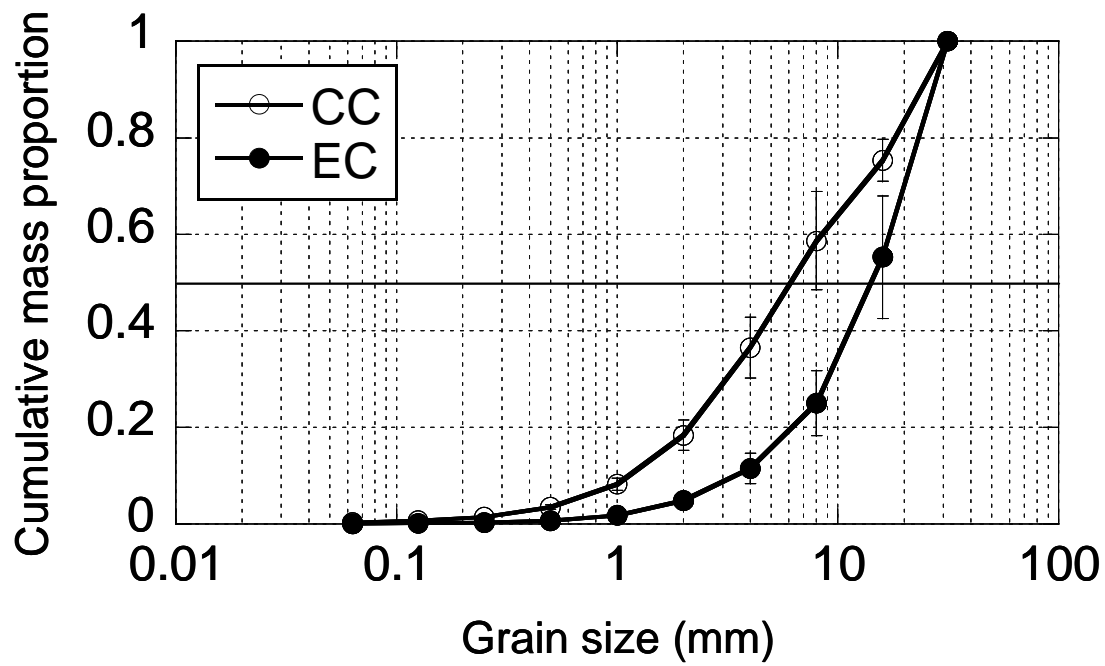


Fig. 5

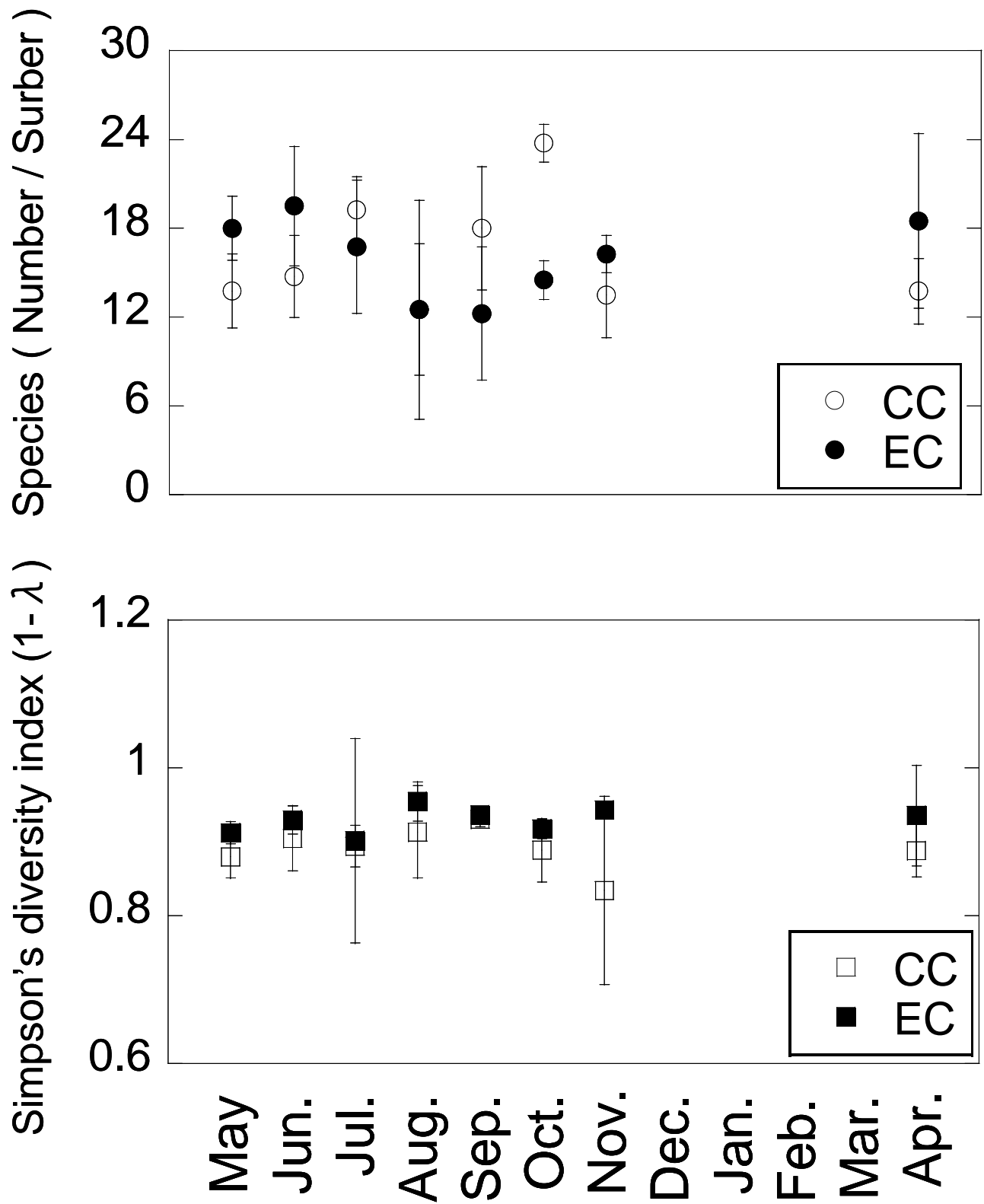
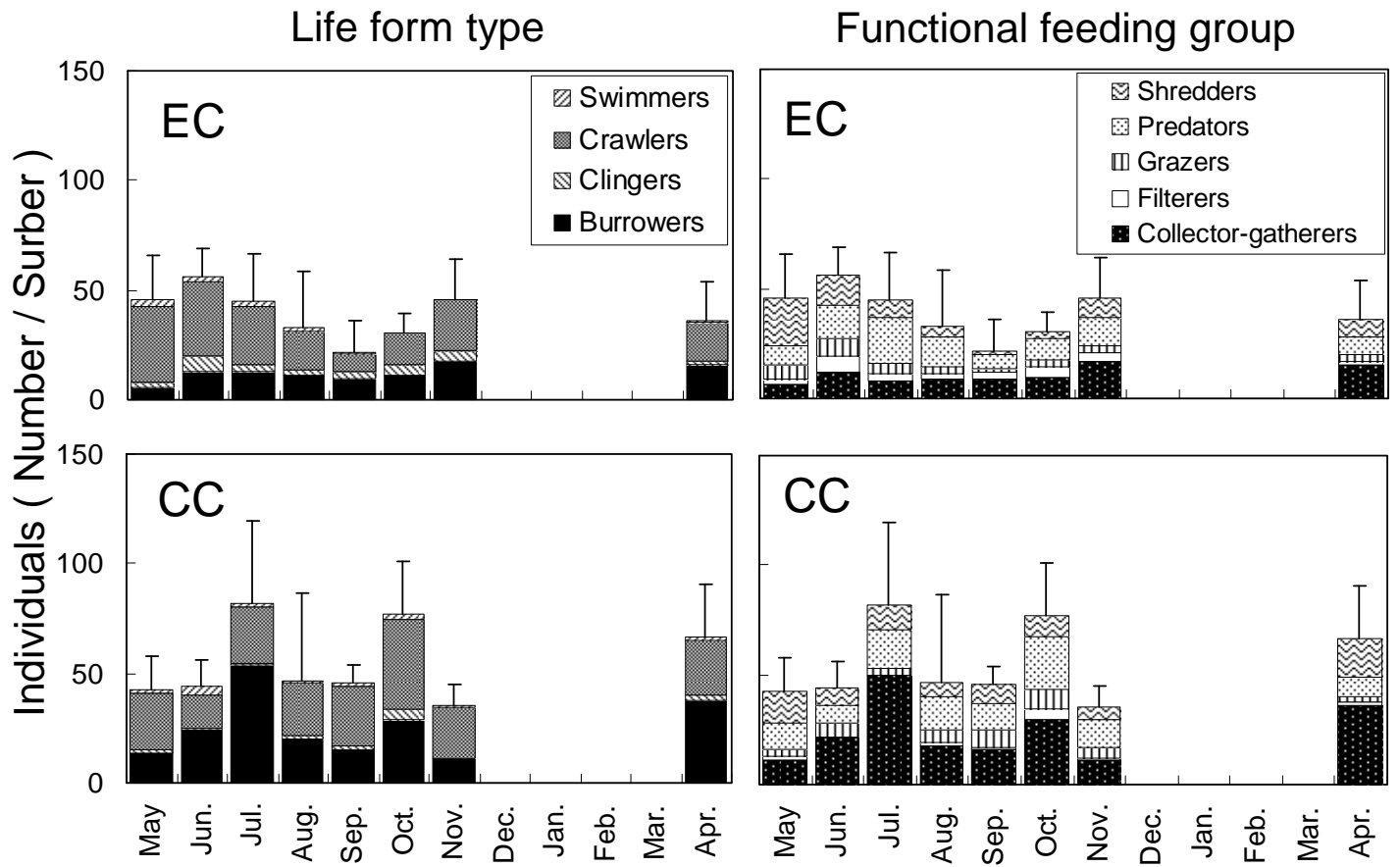


Fig. 6



Title: Indirect effects of excessive deer browsing through understory vegetation on stream insect assemblages.

Authors: Masaru Sakai, Yoshihiro Natuhara, Ayumi Imanishi, Kensuke Imai, Makoto Kato

ESM_S1 Coverage of understory plant species at the exclosure catchment and control catchment in the belt transect survey.

Family	Plant species	Life form ¹	Deer herbivory ²	Coverage ³		Family	Plant species	Life form ¹	Deer herbivory ²	Coverage ³	
				EC	CC					EC	CC
Lycopodiaceae	<i>Lycopodium serratum</i>	P	-	1	-	Rosaceae	<i>Rubus illecebreus</i>	S	+	2	-
Aspleniaceae	<i>Asplenium sarelii</i>	P	+	-	1	Rosaceae	<i>Rubus palmatus</i> var. <i>palmatus</i>	S	+	1	-
Blechnaceae	<i>Blechnum nipponicum</i>	P	+	1	1	Oxalidaceae	<i>Oxalis griffithii</i>	P	+	1	1
Demnstaediaceae	<i>Demnstaedia scabra</i>	P	-	1	2	Anacardiaceae	<i>Rhus ambigua</i>	L	+	1	1
Dryopteridaceae	<i>Arachniodes standishii</i>	P	+	1	-	Anacardiaceae	<i>Rhus trichocarpa</i>	T	+	1	1
Dryopteridaceae	<i>Polystichum triperon</i>	P	+	1	-	Aceraceae	<i>Acer amoenum</i> var. <i>matsumurae</i>	T	+	1	1
Plagiogyriaceae	<i>Plagiogyria matsumureana</i>	P	+	1	1	Aceraceae	<i>Acer micranthum</i>	T	+	1	1
Thelypteridaceae	<i>Stegogramma pozoi</i>	P	+	1	-	Aceraceae	<i>Acer mono</i>	T	+	1	-
Woodsiaceae	<i>Athyrium clivicola</i>	E	+	1	-	Aceraceae	<i>Acer rufinerve</i>	T	+	1	-
Woodsiaceae	<i>Athyrium vidalii</i>	P	+	1	-	Aquifoliaceae	<i>Ilex crenata</i> var. <i>pulidosa</i>	T	+	1	1
Cephalotaxaceae	<i>Cephalotaxus harringtonia</i> var. <i>nana</i>	S	+	-	1	Aquifoliaceae	<i>Ilex pedunculosa</i>	T	-	1	-
Taxodiaceae	<i>Cryptomeria japonica</i> var. <i>radicans</i>	T	-	1	1	Calatraceae	<i>Celastrus orbiculatus</i>	L	+	1	-
Cyperaceae	<i>Carex dolichostachya</i>	P	+	1	1	Vitaceae	<i>Ampelopsis glandulosa</i> var. <i>heterophylla</i>	V	+	1	-
Cyperaceae	<i>Carex japonica</i>	P	+	1	-	Violaceae	<i>Viola grypoceras</i>	P	+	1	-
Dioscoreaceae	<i>Dioscorea japonica</i>	V	+	1	-	Onagraceae	<i>Circaea erubescens</i>	P	+	1	-
Liliaceae	<i>Disporum smilacinum</i>	P	+	1	-	Cornaceae	<i>Aucuba japonica</i> var. <i>borealis</i>	S	+	1	-
Liliaceae	<i>Polygonatum</i> sp.	P	+	1	-	Cornaceae	<i>Swida controversa</i>	T	+	-	1
Liliaceae	<i>Smilax riparia</i> var. <i>ussuriensis</i>	P	+	1	-	Araliaceae	<i>Eleutherococcus sciadophylloides</i>	T	+	1	1
Orchidaceae	<i>Calanthe reflexa</i>	P	+	1	-	Araliaceae	<i>Aralia elata</i>	S	+	1	-
Juglandaceae	<i>Pterocarya rhoifolia</i>	T	+	1	-	Araliaceae	<i>Evodiapanax innovans</i>	T	+	1	-
Betulaceae	<i>Betula grossa</i>	T	+	1	-	Apiaceae	<i>Hydrocotyle maritima</i>	P	+	1	-
Betulaceae	<i>Carpinus japonica</i>	T	+	1	-	Diapensiaceae	<i>Schizocodon soldanelloides</i> var. <i>magnus</i>	P	-	1	2
Betulaceae	<i>Carpinus laxiflora</i>	T	+	1	1	Clethraceae	<i>Shortia uniflora</i> var. <i>kantoensis</i>	P	+	1	1
Fagaceae	<i>Castanea crenata</i>	T	+	1	-	Ericaceae	<i>Clethra barbinervis</i>	T	+	1	-
Fagaceae	<i>Fagus crenata</i>	T	+	1	1	Ericaceae	<i>Monotropastrum humile</i>	P	+	1	-
Fagaceae	<i>Fagus japonica</i>	T	+	1	1	Ericaceae	<i>Elliotia paniculata</i>	S	+	1	-
Fagaceae	<i>Quercus crispula</i>	T	+	1	1	Ericaceae	<i>Pieris japonica</i>	S	+	1	1
Urticaceae	<i>Elatostema umbellatum</i> var. <i>majus</i>	P	+	1	-	Ericaceae	<i>Vaccinium japonicum</i>	S	+	1	1
Polygonaceae	<i>Polygonum thunbergii</i>	A	+	1	-	Ericaceae	<i>Vaccinium oldhamii</i>	T	+	1	-
Polygonaceae	<i>Fallopia japonica</i>	P	+	1	-	Styracaceae	<i>Syrax japonica</i>	T	+	1	-
Magnoliaceae	<i>Magnolia salicifolia</i>	T	+	1	-	Styracaceae	<i>Syrax obassia</i>	T	+	1	-
Lauraceae	<i>Lindera erythrocarpa</i>	T	+	1	-	Symplocaceae	<i>Symplocos coreana</i>	S	-	1	1
Lauraceae	<i>Lindera umbellata</i> var. <i>umbellata</i>	S	+	1	1	Oleaceae	<i>Fraxinus sieboldiana</i>	T	+	1	-
Theaceae	<i>Eurya japonica</i>	S	+	1	-	Gentianaceae	<i>Tripterospermum iaponicum</i>	L	+	1	-
Hamamelidaceae	<i>Hamamelis japonica</i> var. <i>obtusata</i>	T	+	1	1	Boraginaceae	<i>Trigonotis brevipes</i>	P	+	1	-
Saxifragaceae	<i>Astilbe thunbergii</i>	P	+	1	-	Ramiaceae	<i>Plectranthus longitubus</i>	P	+	1	-
Hydrangeaceae	<i>Hydrangea hirta</i>	S	+	2	1	Verbenaceae	<i>Callicarpa japonica</i>	S	+	1	-
Hydrangeaceae	<i>Hydrangea paniculata</i>	S	+	2	1	Caprifoliaceae	<i>Sambucus sieboldiana</i>	S	+	1	-
Hydrangeaceae	<i>Schizophragma hydrangeoides</i>	L	+	1	1	Caprifoliaceae	<i>Weigela hortensis</i>	S	+	1	-
Rosaceae	<i>Pourthiaea villosa</i>	S	+	1	-	Campanulaceae	<i>Peracarpa carnososa</i>	P	+	1	-
Rosaceae	<i>Padus grayana</i>	T	+	1	-	Asteraceae	<i>Carpesium abrotanoides</i>	P	+	1	-
Rosaceae	<i>Prunus incisa</i> ssp. <i>kinkiensis</i>	T	+	1	1	Asteraceae	<i>Carpesium divaricatum</i>	P	+	1	-
Rosaceae	<i>Rubus crataegiifolius</i>	S	+	1	-	Asteraceae	<i>Cirsium ashinense</i>	P	+	1	-

¹Life form: E, epiphyte; L, liana; P, perennial; S, shrub; T, tree; V, vine.

²Deer herbivory: +, edible; -, inedible.

³Coverage: -, no cover; 1, 0-25%; 2, 25-50%; 3, 50-75%; 4, 75-100%.

Title: Indirect effects of excessive deer browsing through understory vegetation on stream insect assemblages.

Authors: Masaru Sakai, Yoshihiro Natuhara, Ayumi Imanishi, Kensuke Imai, Makoto Kato

ESM_S2 List of families and genera of aquatic insects of overall samples in all months recorded at the exclosure catchment and control catchment.

Order	Family or genus	EC	CC	Order	Family or genus	EC	CC
Ephemeroptera	<i>Ameletus</i>	2	1	Diptera	<i>Ablabesmyia</i>	0	1
	<i>Baetiella</i>	1	2		<i>Antocha</i>	2	0
	<i>Baetis</i>	39	44		Athericidae	2	0
	<i>Bleptus</i>	3	0		Ceratopogonidae	10	48
	<i>Cinygmula</i>	7	3		<i>Conchapelopia</i>	27	13
	<i>Dipteromimus</i>	5	2		Diamesinae	22	64
	<i>Ecdyonurus</i>	64	108		<i>Dicranota</i>	6	9
	<i>Epeorus</i>	2	1		<i>Dixa</i>	3	5
	<i>Ephemerella</i>	129	298		<i>Epoicocladus</i>	50	80
	<i>Ephemerella</i>	1	1		<i>Haxatoma</i>	2	0
	<i>Heptagenia</i>	2	0		<i>Limnophila</i>	21	14
	<i>Paraleptophlebia</i>	81	149		Limoniinae	2	1
	<i>Proclonia</i>	1	0		<i>Neobrylia</i>	4	2
	<i>Rhithrogena</i>	2	1		Orthocladinae	18	120
	<i>Aeshna</i>	1	0		<i>Pedicia</i>	9	4
Odonata	<i>Anotogaster</i>	1	11		<i>Pentaneura</i>	2	3
	<i>Davidius</i>	4	8		<i>Pilaria</i>	0	1
	<i>Epiophlebia</i>	0	1		Simuliidae	0	1
	<i>Gomphus</i>	0	1		<i>Suragina</i>	3	1
	<i>Lanthus</i>	1	4		Tabanidae	21	58
	<i>Mnais</i>	1	5		Tanypodinae	6	6
	<i>Planaeschna</i>	3	8		<i>Tanytarsus</i>	11	116
	<i>Polycanthagyna</i>	2	0		<i>Tipula</i>	17	5
	<i>Amphinemura</i>	65	29		<i>Tvetenia</i>	1	0
	<i>Caroperla</i>	82	156	Trichoptera	<i>Agapetus</i>	8	6
Plecoptera	<i>Haploperla</i>	31	13		<i>Apatania</i>	0	1
	<i>Isoperla</i>	1	3		<i>Arctopsyche</i>	2	0
	<i>Kiotina</i>	1	0		<i>Brachycentrus</i>	3	0
	Leuctridae	22	18		<i>Diplectrona</i>	2	0
	<i>Nemocapnia</i>	1	0		<i>Dolophilodes</i>	30	22
	<i>Nemoura</i>	123	138		<i>Glossosoma</i>	1	0
	<i>Niponiella</i>	13	47		<i>Goera</i>	3	0
	<i>Protonemura</i>	10	0		<i>Hydropsyche</i>	79	25
	<i>Pseudomegarcys</i>	0	1		<i>Lepidosotma</i>	30	44
	<i>Sweltsa</i>	3	2		<i>Leptocerus</i>	0	2
Megaloptera	<i>Togoperla</i>	110	56		<i>Micrasema</i>	2	0
	<i>Parachauliodes</i>	12	9		<i>Perissoneura</i>	14	45
	<i>Protohermes</i>	1	0		<i>Plectrocnemia</i>	0	1
	<i>Sialis</i>	1	8		<i>Psilotreta</i>	3	63
Hemiptera	<i>Mesovelina</i>	1	0		<i>Rhyacophila</i>	25	21
Coleoptera	<i>Dryopomorphus</i>	2	0		<i>Setodes</i>	2	0
	<i>Eubrianax</i>	14	13		<i>Wormaldia</i>	2	1
	<i>Hydrocyphon</i>	0	1				
	<i>Paralichas</i>	59	32				
	<i>Pseudamphihi</i>	1	1				
	<i>Sacodes</i>	2	1				